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Thirty years of ecological research at the Gran Sasso d'Italia LTER site: climate change in action

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Abstract

Since 1986, vegetation monitoring of alpine plant communities has been performed at the Gran Sasso d'Italia LTER site (https://deims.org/c0738b00-854c-418f-8d4f-69b03486e9fd) in the Central Apennines, through phytosociological relevés and abundance and coverage estimation of the vascular flora at fine scale. The monitoring activities for abiotic parameters regard air and soil temperatures, rainfall, snowfall and snow cover persistence.

A comparative analysis of changes in species composition, life forms, life strategies and morpho-functional types allowed recognition of dynamical processes (fluctuation and degeneration) and an increase in stress- and drought-tolerant and ruderal species, probably linked to a general process of climate change.

A trend of variation forced by increasing drought was recorded in high-mountain plant communities, normally within a dynamic fluctuation process. There has been a 50–80% change in species composition with respect to the total number of species observed over the years. Whereas the total number of species has increased in all communities, in high-mountain mesic grassland 20% of sensitive species have completely disappeared. Early signs of a degeneration process were already discernible after seven years: such signs are more evident in snow-dependent communities, with a quantitative increase in more thermophilic and drought-tolerant species and a parallel decrease in more mesic, cryophilic and competitive species. In particular, the following phenomena have been recorded in high-mountain mesic grassland, in agreement with predicted or observed phenomena in other Alpine or Arctic areas: (a) coverage increase (or appearance) of ruderal and stress- and drought-tolerant species; (b) coverage decrease (or disappearance) of cryophilic, mesic and competitive species.

These short-term changes could lead, in the medium- or long-term, to a disgregation process affecting the high elevation plant communities of the Apennines (including the local extinction of most of the cold-adapted species), due to their very low resilience. The phenomena described may be linked to the observed climate change which occurred during the last century (in particular in the last 50 years) in the Apennines, consisting mainly, in the mountains, of a strong reduction in the duration of snow-cover and an increase in mean and minimum annual temperatures.

Keywords
LTER, climate change, alpine plant communities, Apennines, Braun-Blanquet approach

Introduction

According to the latest IPCC reports (2007, 2014), the current climate change is expected to cause, by the end of this century, a global average temperature increase between 1.8 and 4 °C. This warming is constantly accelerating, especially at middle and high latitudes which are experiencing a much higher rate. Climate change will become more marked in Southern Europe, in particular in the central-southern part of the Italian Peninsula (Mathez 2009), where a steep reduction in precipitation (20–30% ca.) and a strong increase in temperature (3.0–4.0 °C ca.) are expected in the next 80 years. High-resolution climate simulations (based on IPCC scenario RCP4.5, stabilization without overshoot pathway) predict for Italy in 2100 a marked reduction in total summer precipitation (June-August) of 24% and a decrease in snow coverage (h>1 cm) of 21 days/year and in frost days (t<0 °C) of 20 days/year (Bucchignani et al. 2016, Zollo et al. 2016). Recorded data for this part of Italy in the last ca. 100 years (Buffoni et al. 1999, Brunetti et al. 2000a, b) confirm this trend, with 15% less rainfall and temperatures 1 °C above average values, to the extent that the present Mediterranean-mountain climate may be described as shifting to a climate with definite Mediterranean characteristics, with precipitation peaks only in winter and snowfall becoming rarer. In addition, remote sensing data (IPCC 2001, 2007, 2014) show that the extension of yearly snow coverage has decreased by 10% in the last 50 years in all regions of the Northern Hemisphere. Data collected for the Italian Alps on the ground (meteorological stations) confirm a 30-year trend toward a decrease of snowfall, snow depth and coverage (Cannone et al. 2007).

Observed global climate warming in the 20th century (+0.7 °C in the last 60 years, +0.1 °C per decade in the same period, IPCC 2014) has already altered the vascular plant diversity at many high-elevation sites in the Alps (Braun-Blanquet 1955, 1957, Hofer 1992, Grabherr et al. 1994, 1995, 2001, Gottfried et al. 2002, Camenisch 2002, Pauli et al. 2003a, b, Walther et al. 2005, Pauli et al. 2007, Holzinger et al. 2008, Vittoz et al. 2008, Parolo and Rossi 2008, Erschbamer et al. 2009, 2011) and in other European mountain ranges (Klanderud and Birks 2003, Moiseev and Shiyatov 2003, Virtanen et al. 2003, Petriccione 2005, Steinbauer et al. 2018). Several modelling approaches focusing at large scale (Thuiller et al. 2005) and local scale within the Alps

and the Apennines have suggested remarkable warming-induced threats for reducing alpine plant diversity (Gottfried et al. 1999, Guisan and Theurillat 2000, Theurillat and Guisan 2001, Dirnböck et al. 2003, Stanisci et al. 2006, Frate et al. 2018). A significant decrease of vegetation coverage and an increase in species richness, with the associated lack of half of the original species and coverage decline of the most dominant species, have been found in the Central Alps in subalpine, alpine and nival plant communities in the last 50 years (Cannone et al. 2007, Cannone and Pignatti 2014). A general increase in the plant cover of most species (although not significant) has been recognized in some alpine and subalpine LTER sites in Austria, Switzerland and Italy in the montane, subalpine and alpine belts in the last 20 years (Rogora et al. 2018).

As far as the Central Apennines (Italy) is concerned, data collected at some key meteorological stations show a considerable recent decrease in precipitation (especially in spring and autumn) and a small increase in average temperature (Petriccione 2005). Snowfall data (Baldoni et al. 1999, Romeo and Scarpelli 2001) confirm the general trend, with a clear decrease in the last 80 years. The same trends are also recognizable in other localities, confirming the observed general trend towards drought conditions in Central and Southern Italy. These recorded and predicted changes are already producing noticeable effects of drought in most of the biocenoses distributed in the Mediterranean bio-climatic zone. On Mediterranean high mountains, the most endangered plants are the cryophilic species with a distribution range centred over the timberline in the alpine belt, showing morphological and functional adaptations to the severe physical environment of high elevation mountains (Körner 1999). Accordingly, alpine plant communities in this zone can be regarded as sensitive indicators of climate change (Körner 1994). Nevertheless, only a small number of papers have been published on this topic and those based on specific field observations are even less abundant. A first attempt to analyse possible shifts in the vegetation belts of Italy caused by climate change (Blasi 1996) considers only theoretical models based on small-scale bio-climatic maps. An extensive review of the possible impacts of climate change on sensitive land ecosystems in Italy predicts a short- and medium-term process of degeneration for most of the analysed biocenoses, with a gradual long-term transformation towards more drought-tolerant biocenoses (Petriccione 1995). Other studies start from the same approach, but the major emphasis is placed on especially sensitive biocenoses in Italy (Petriccione and Claroni 1996, Petriccione et al. 1998): the plant communities analysed are soil-controlled (flood-plain forests and marsh communities) or high-altitude biocenoses (sub-alpine shrubland and alpine tundra). For most of these communities, a medium-term process of degeneration is predicted, followed by a long-term process of regression. Since 1993, a trend of variation forced by increasing drought has been recorded in all plant communities above the timberline, normally within a dynamic fluctuation process. There has been a 10–20% change in species composition with respect to the total number of species observed over nine years (Petriccione 2005). Early signs of a degeneration process were already discernible after seven years: such signs are more evident in snow-dependent communities, with a quantitative increase in more thermophilic, drought- and stress-tolerant species and a parallel decrease in

more mesic, cryophilic and competitive species. In particular, the following phenomena have been recorded in alpine tundra, high-mountain mesic and snow-bed grassland, in agreement with predicted or observed phenomena in other Alpine or Arctic areas (Chapin et al. 1996, Theurillat and Guisan 2001, Welker et al. 2001): (a) coverage increase (or appearance) of chamaephytic, drought- and stress-tolerant species; (b) coverage decrease (or disappearance) of hemicryptophytic, cryophilic, mesic and competitive species. Another clearly-recorded effect of global warming on high elevation plant diversity is also the shift of some species from lower to higher altitudinal ranges. In the alpine belt of the Majella massif in the Central Apennines, the warmer eastern slopes are the first to be affected by the colonization of thermophilic species, whereas the north-facing exposures, with a shorter frost-free period, are the most conservative, showing greater inertia to the invasion process (Stanisci et al. 2005). Several species typical of the subalpine belt at their upper altitude limit, not recorded in previous studies, were mainly found on east-facing exposures. The species invasion process is able to modify the ecosystem functions, increasing fragmentation of habitats suitable for the survival of cryophilic species. Prediction models (GLM) in the Central Apennines (Stanisci et al. 2006) indicate a decline of alpine tundra affecting 75% of its current area, in relation to an increase in mean temperature of 1 °C. The predicted decline of the alpine belt in the Apennines will change the diversity pattern of plant species and communities in high elevation habitats with a strong extinction risk for local endemic cryophilic species. Over the last four decades, a significant increase in the frequencies of thermophilic, mesonitrophilic, caespitose hemicryptophytes and suffruticose chamaephytes has been detected in the alpine belt at an LTER site in the Central Apennines (Evangelista et al. 2016, Stanisci et al. 2016). Moreover, in the Northern Apennines a degeneration process was observed in chionophilic species (Rossi et al. 2004).

This paper is based on continuous ecological observations performed at an alpine research site ("Gran Sasso d'Italia", https://deims.org/c0738b00-854c-418f-8d4f-69b03486e9fd) established in 1986 and joining the LTER Italy network in 2007. The longest data series of vegetation data in the Apennines is available at this site, including up to 33 years of observations at community level. At European level, only data at species level are available for so long a time, except for an area in the Italian Alps (Stelvio National Park) where a 50-year data series is available (Cannone and Pignatti 2014). The site is part of the "Apennines: high elevation ecosystems" LTER site, which consists of "orographic islands" of alpine biocenoses in the central Mediterranean basin, along the Apennine chain, where many endemic and rare taxa occur. This species pool is critically endangered by climate warming, as reported in several studies (Petriccione 1995, Petriccione and Claroni 1996, Petriccione et al. 1998, Grabherr et al. 2001, Pauli et al. 2001, Petriccione 2005, Rossi et al. 2009, Stanisci et al. 2006, Gottfried et al. 2012). The first 18–25 years of observations at this site show a clear tendency of the high altitude plant communities to adapt to aridity (Petriccione 2012). A current process of gradual degeneration has been recognised, with a marked reduction in rare species adapted to colder climates and the invasion of more thermophilic species. Only 44–50% of the total number of species has survived with no significant changes,

whereas 40% are invaders. The remaining species were no longer found in the research plots (Petriccione 2012). The main purpose of the research site is to investigate and monitor structure and composition changes in plant communities in relation to climate change. The aim of this paper is to attempt to answer four questions: a) Are plant communities changing over time? b) Toward a new equilibrium? c) Are species responding in different ways? d) Is there a relationship between the changes in the features of the communities and the predicted and/or observed changes in the temperature and precipitation regimes?

Materials and methods

Study area

The LTER site EU IT 01-003-T "Appennino Centrale: Gran Sasso d'Italia", established in 1985, covers an area of ca. 0.5 km^2, with an elevation range from 2130 to 2385 m a.s.l. (approx. latitude 42°26N and longitude 13°33E, Suppl. material 1, Figure S1). The Gran Sasso d'Italia massif is located in the Central Apennines, which reach their highest elevation with the Gran Sasso peak (2914 m a.s.l.). The research site, one of the highest in Italy, has been a protected area both at National (as a National Park) and European level (as part of the EU Natura 2000 Network) since 1995. Land use in the site has remained unchanged over the last 50–100 years (personal observations, Falcucci et al. 2007): the only relevant activities are based on winter sports (a small ski resort is located at the southern boundary of the site), mountaineering and, more recently, nature tourism, all with very low impact on plant communities. In the past, land use was based on transhumant sheep farming, in progressive and rapid abandonment after the major political and economic change affecting Italy at the end of the 19th century (Clementi 1995). As a result, land management has not changed significantly, at least not since 1986, the year of ecological research at the site began.

The climate is Mediterranean-mountain (Pignatti 1969, Petriccione 2005), with an average annual temperature of 3.7 °C, average annual precipitation of 1170 mm, maximum rainfall in spring and autumn, no drought period in summer, but an extreme and prolonged frost period in winter, for 5–6 months, with prolonged snow cover for more than 6 months a year. The average monthly maximum temperature is not very high (17.4 °C), whereas the average monthly minimum temperature is very low (- 8.9 °C).

Since 1986, the same ecologists (first from the Universities of Rome and L'Aquila, from 1999 the Corpo Forestale dello Stato (National Forest Service) and since 2017 the Biodiversity and Park Protection Department of the Carabinieri) have been continuously studying the state of the high elevation vegetation, analysing all the plant species present in permanent plots where surveys are carried out once a year. Since 2013, the microclimate has also been studied directly using automatic temperature measurement devices installed in the soil.

The site consists of high elevation plant communities above the timberline, in the central Mediterranean basin, along the Apennine mountain range, included in the alpine and Mediterranean high-mountain altitudinal belts (Petriccione and Persia 1995). They belong to two habitat types protected by EU Habitat Directive no. 92/43/EEC and listed in its Annex I (attribution to EU habitat types according to Biondi et al. 2009 and personal observations). Two biocenoses are studied in detail, both described by Petriccione and Persia (1995) and characterized by perennial species, particularly well adapted to cold and drought conditions, with high resistance, but very low resilience: (a) high-mountain primary dry grassland (*Pediculari elegantis-Seslerietum tenuifoliae*, corresponding to habitat "6170 – Alpine and subalpine calcareous grasslands"), with non-continuous plant coverage, occurring between 2000 and 2300 m a.s.l. in the Central and Southern Apennines, in wind-swept peak and ridge zones with spatially limited and temporally discontinuous snow-cover, below zero night temperatures for ca. eight months a year and intensive cryo-nival phenomena (ice needles) in all seasons (except for the summer); soil is shallow (ca. 20 cm) and pH is basic (7.20–7.50, Furrer and Furnari 1960, Suppl. material 1, Figure S2); (b) high-mountain primary mesic grassland (*Luzulo italicae-Festucetum macratherae*, corresponding to the priority habitat "6230* – Species-rich *Nardus* grasslands, on siliceous substrates in mountain areas and submountain areas in Continental Europe"), with continuous plant coverage, occurring between 2000 and 2400 m a.s.l. throughout the Central Apennines, in wind-free zones with snow-cover for ca. six months a year, below zero night temperatures for ca. eight months a year and the absence of crio-nival phenomena (due to the prolonged snow-cover); soil is deep (cm 35–55 ca.) and pH is acid (4.50–5.90, Furrer and Furnari 1960, Suppl. material 1, Figure S3). The two plant communities are sampled on the basis of six permanent plots (three plots for each community), each measuring 100 m^2, grouped in two three-plot clusters, representative of a larger area of ca. 0.5 km^2. The site parameters observed include primary producers (species frequency and abundance, yearly) and microclimate (soil temperature, hourly, throughout the year). Some information on the microclimate characteristics of the *Pediculari-Seslerietum* community are already available for that specific site, although only for one summer season (Brucculeri and Petriccione 1994): the maximum recorded temperature is 27.5 °C.

Climate data

Climate data were collected at the official Campo Imperatore meteorological station (2135 m a.s.l.), located in the Gran Sasso d'Italia mountains, with over 70 years of standard precipitation and temperature observations (since 1942). Data on snow precipitation and the height of snow cover in winter were collected at the non-automatic METEOMONT station (managed by the Carabinieri, formerly the National Forest Service) at the same location, from 1988 to 2016. Total winter snow precipitation has been calculated on the basis of METEOMONT data (daily visual observations of height of new snow cover, in cm, assuming 1 cm of snow equal to 1 mm of liquid precipitation).

Continuous soil microclimate observations have been made at the site since 2013, by means of two data loggers in the soil (-10 cm depth), one for each community, according to the GLORIA methodology (Pauli et al. 2004). Near-surface ground temperature is a good proxy for the presence/absence of snow cover and therefore for tracking the related no-frost winter days (Lundquist and Lott 2008, Schmid et al. 2012). Unfortunately, several failure events affected one of the loggers and therefore data for the *Luzulo-Festucetum* is only available for 3 years (2013–2015, including two winters); in contrast, a valuable data series is available for the *Pediculari-Seslerietum* (5 years, from 2013 to 2018, including 5 winters). Climate data were analysed by linear regression model, using mean annual temperature, total annual precipitation, mean winter snow depth and total winter snow precipitation as response variables and "year" as explanatory variable. When data did not meet the model assumptions, non-parametric linear regression was used. The significance of the regressions was assessed using the F-test and the Theil-Sen test for simple linear regression and non-parametric linear regression, respectively.

Analysis at community level

For each of the six plots, 100 m^2 in area, a phytosociological relevé was performed (according to the Braun-Blanquet approach) in 1993 and repeated 6, 8 and 15 years later, in 1999, 2001 and 2008, on the same fixed surface area of the entire plot. Since 2008, data collection has been yearly, including three plots per community. In one case (*Pediculari-Seslerietum*), a relevé had also been performed seven years earlier (in 1986), even if in only one plot. All data are reported in Suppl. material 1, Table S1 (*Pediculari-Seslerietum* 1986–2017) and 2 (*Luzulo-Festucetum* 1993–2017). The coverage scale is according to Braun-Blanquet (1932, 1964), as modified by Pignatti (1952). Species nomenclature is according to Pignatti (2017–2019).

The ecology and distribution range of each plant community are described according to Petriccione (1994) and Petriccione and Persia (1995). The dynamical current tendencies (according to Falinski 1986, 1989) in each community were identified by indicator species (as reported by Petriccione and Claroni 1996).

Species composition changes were calculated by simply comparing year by year, each year with the original species composition (at 1986 or 1993) and with all species occurring during the 25–33 years of observation.

A temporal trend analysis of species composition, life forms (Raunkiaer 1934), life strategies (Grime 1977, 1984, 1996) and morpho-functional types (defined ad hoc, according to an inductive approach, Woodward and Cramer 1996) was performed for each community, on the basis of the relative number of species per group. On the basis of an ad hoc quali-quantitative checklist of easily recognizable morphological characteristics (occurring on leaves and stems), a multivariate analysis helped define four morpho-functional groups, named after their key characteristics: reptant (Rp), graminoid hemicryptophytes (Hgr), scapose and rosulate hemicryptophytes (Hsr) and

crassulent (Cr). Plant functional traits are considered as good predictors of community changes (Lavorel and Garnier 2002). All traits (directly measured in the field), are reported in Suppl. material 1, Table S1 *(Pediculari-Seslerietum* 1986–2017) and 2 *(Luzulo-Festucetum* 1993–2017).

To analyse changes over time at community level, the species cover value for each plot (Pignatti 1952) and for each year was transformed into percentage values, according to the following criteria (+: 1%, 1: 10%, 2: 30%, 3: 50%, 4: 70% and 5: 90%). Analysis of the communities was based on taxonomic diversity and functional structure, including life strategies (Grime 2006) and ecological features. In the first case, three taxonomic diversity indices were calculated: species richness, evenness and Simpson index. For functional and ecological analysis, we calculated the community weighted mean (hereafter CWMs), following the equation of Garnier et al. (2004):

$$CWM = \sum_{i=l}^{S} p_i x_i$$

where x_i is the mean trait values and pi is the relative abundance of the *i*-th species. To calculate the CWM with trait (hereafter CWM_{trait}) the matrixes "relevés x species (cover %)" and "species x trait values" were used. This index can be adequately used to quantify the relationship between a given trait and certain environmental conditions. The variation in life strategies was also approached using the above equation, multiplying the matrix "relevés x species (cover %)" with the matrix "species x Grime's strategy" using the same equation of Garnier et al. (2004) to weight life strategies at community level (hereafter CWM_{Grime}). For categorical traits, the relative frequency (%) of each trait state was obtained, while for continuous traits (such as plant height and leaf width), a single trait value was referred to the community mean value of that trait. In the case of species with multiple Grime's strategy, all strategies were computed separately, considering the contribution of each species to the community features according to its strategies.

Finally, an analysis of the change over time of the community's ecological features was performed using the ecological bioindicator values (hereafter BV) for the Italian flora (Pignatti 2005) to analyse changes in environmental conditions separately for both communities. The mean ecological indicator at community level was calculated in the same way as for CWM, by multiplying the matrix "relevés x species (cover %)" with "species xBV", to obtain a matrix "relevés x BV" (hereafter CWM_{BV}). Ecograms for the two plant communities were generated, as suggested by Pignatti (2005). Taxonomic diversity indices (Simpson, Species richness, Evenness), CWM_{trait}, CWM_{Grime} and CWM_{BV}were calculated for each observation year and for each community to assess the effects of temporal changes on different community facets (i.e. taxonomic, functional, Grime's live strategy and ecological) separately for the *Pediculari-Seslerietum* and *Luzulo-Festucetum*. A single linear regression model was developed, using as response variable each index separately and "year" as explanatory variable. The same approach was followed for the climatic analysis: a linear regression model was developed and the model assumption was verified. If the data did not meet the assumptions, a non-parametric linear regression model was used. The test results were corrected for multiple comparisons using Holm's correction to avoid Type I error.

Analysis at species level

At species level, changes in the cover of dominant and other selected species were analysed for both communities along a continuous temporal gradient (as performed by Evangelista et al. 2016, although along a non-continuous temporal gradient). For the *Pediculari-Seslerietum,* the analysis was performed on *Sesleria juncifolia*, *Carex kitaibeliana*, *Globularia meridionalis* (dominant), *Juniperus sibirica* (becoming dominant) and *Gymnadenia conopsea* (invader); for the *Luzulo-Festucetum*, on *Festuca violacea*, *Poa alpina* (dominant), *Carex caryophyllea*, *Trifolium pratense* (becoming dominant), *Trifolium thalii* (former dominant), *Silene ciliata* (mesophytic) and *Anthyllis montana* (xerophytic). In this case, species cover values were used as response variable and "year" as explanatory variable.

The same statistical method as described above was employed and a non-parametric linear regression model was used when the assumptions for the parametric model were not satisfied.

All the analyses were computed using R software (version 3.4.4, R Foundation for Statistical Computing, R Core Team 2015). The *stats* package (lm function) was used for the parametric linear regressions and the *mblm* packages version 0.12 (mblm function) for the non-parametric regression. CWMs were computed with the functcomp function in the FD package version 1.0–12 in R, otherwise taxonomic indices were computed with diversity function in the vegan package. For the Simpson index, the "Simpson" argument returning 1-D was selected. Finally, the *gvlma* package version 1.0.0.2 (gvlma function) and *stats* package (shapiro.test function) were used to validate the linear model assumptions. Temporal autocorrelation was checked with acf() function in stats package.

Results

Climate

Analysis of precipitation and temperature in the period 1950–2014 (65 years) shows (Fig. 1) an important and significant increase in mean annual temperature (+1.7 °C) and a small and not significant decrease in annual precipitation amount (-30 mm), especially in spring and autumn. Although the temperature trend seems very clear, the precipitation regime, on the other hand, is very variable year by year (with an average of 1170 mm), ranging from a minimum of 568 mm (year 1977) to a maximum of 1612 mm (year 1969), increasing the drought stress in very dry years: in recent decades, this has occurred in 2002, 2010 and 2011, with very low values of 700–800 mm.

For snow data, a significant variation (decrease) was found for snow precipitation only (Fig. 1, -147 mm), but not for the snow depth, which is not directly correlated. As for total precipitation, the snowfall regime is also very variable (Suppl. material 1, Figure S4) year by year (with an average of 163 mm), ranging from a minimum of only 40 mm (winter 2011/2) to a maximum of 309 mm (winter 2002/3), includ-

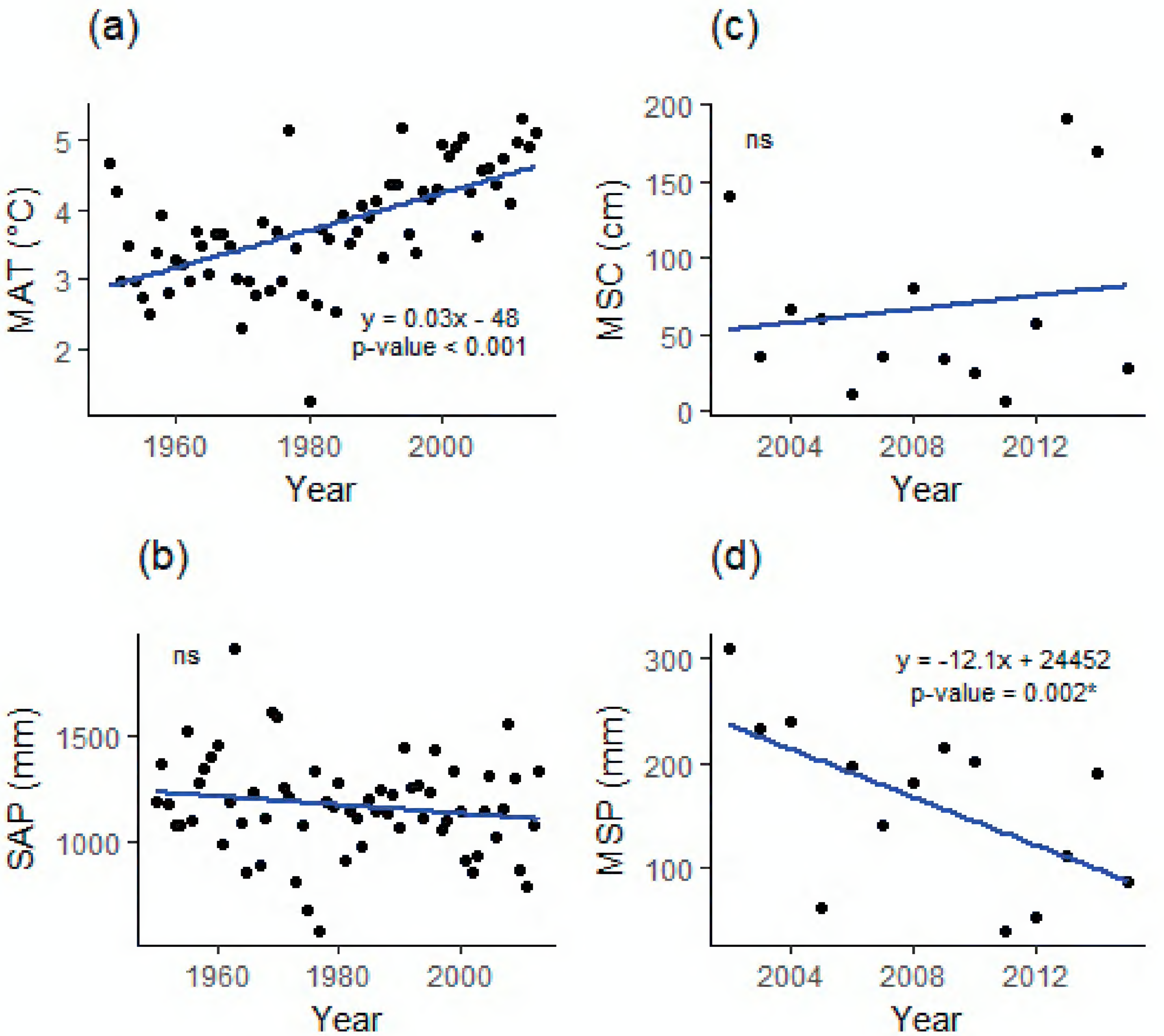

Figure 1. Changes in climate features during the period 1950–2014 at the Gran Sasso d'Italia LTER site (**a** mean annual air temperature (MAT) **b** mean annual total precipitation (SAP) **c** mean winter snow depth (MSC) for the period 1988–2016 **d** total winter snow precipitation (MSP) for the period 1988-2016 (SWE, mm); *: regression performed using non-parametric linear regression analysis; ns: non-significant).

ing frequent winters with mean height of snow cover lower than 20 cm (5 years). In winters with a very low snowfall amount, the height of snow cover (with an average value of 61 cm) reaches very low values (only 6 cm in winter 2011/2), whereas when snowfall is abundant the snow depth can reach very high values (192 and 170 cm in winters 2013/4 and 2014/5). But the snow depth can go down to very low values even in winters with a high snowfall amount, due to rapid and frequent high-temperature peaks, as in winter 2006/7, with 192 mm of snowfall and only 11 cm of snow cover.

The continuous soil microclimate observations performed at the site (Figs 2, 3), in accordance with data provided for only one year by Brucculeri and Petriccione (1994), show marked differences between the two communities. Whereas in winter 2013/4 the

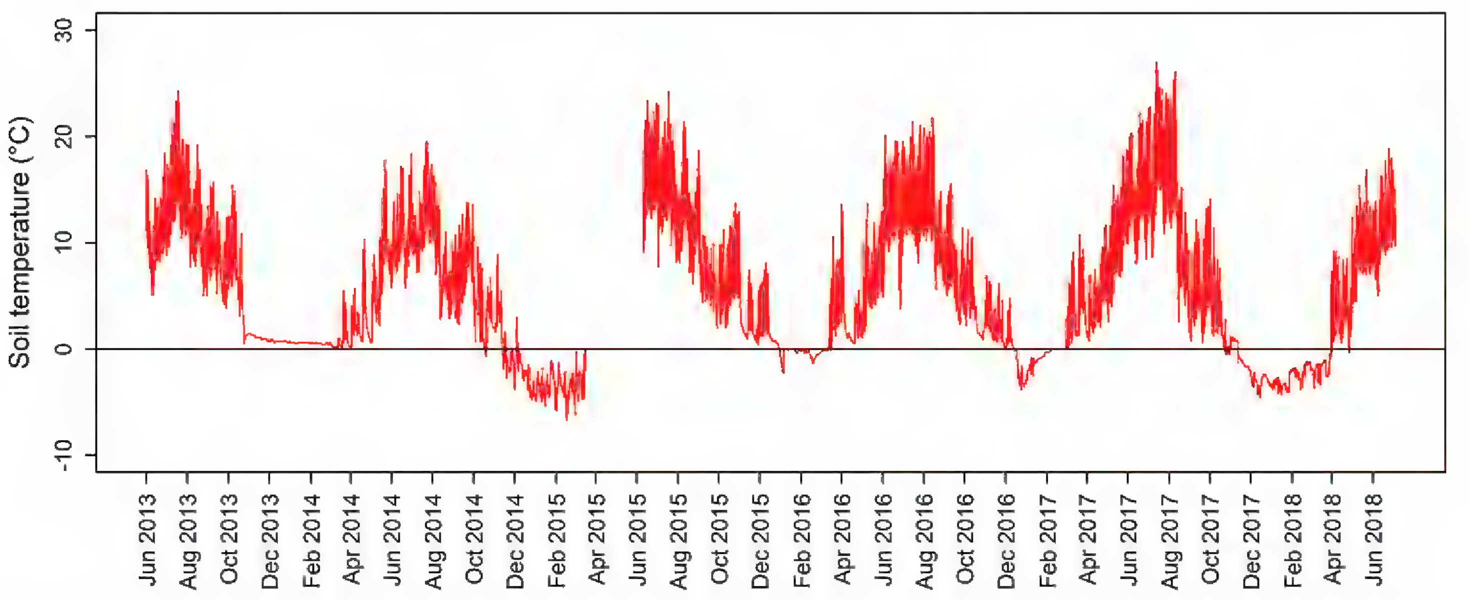

Figure 2. Daily Seasonal and annual changes in soil temperature (°C, recorded on a hourly bases -10 cm depth), at the dry grassland plots (Pediculari-Seslerietum) in the period May 2013-July 2018.

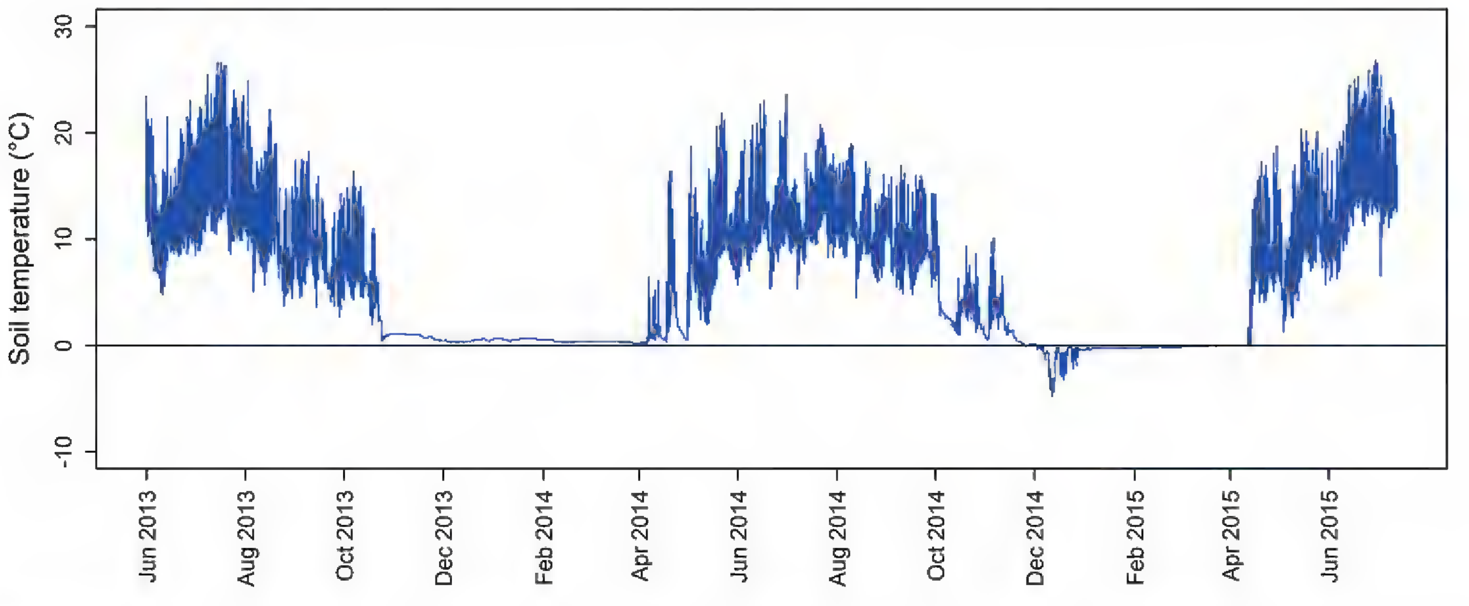

Figure 3. Seasonal and annual changes in soil temperature (°C, recorded on a hourly bases -10 cm depth) at the mesic grassland plots (Luzulo-Festucetum), in the period May 2013-July 2015.

abundant and persistent snowpack preserved the biocenoses from frost episodes (with temperature below 0 °C), in winter 2014/5 a very similar snowfall amount was so discontinuous that the dry grasslands were exposed to frost for 152 days (in other words, all the winter season, with min. absolute temperature up to -6.7 °C) and the sensitive mesic grasslands for 26 days (with min. absolute temperature up to -4.8 °C). The same frost episodes were recorded in the following winters: 8 and 14 days in 2015/6, 24 days in 2016/7 and the full winter season (99 days) in 2017/8, exposing the biocenoses to very dangerous frost stress, with a corresponding increase of mortality of roots and microbial fauna (Edwards et al. 2007)

Community level

Species composition changed by 10–15% per year in the period 1993–2017 (25 years) in both communities; the rate of change is also quite similar if the observation period is extended to a total of 32 years (possible only in the case of the *Pediculari-Seslerietum).* Long-term analysis, however, shows different trends: the dry grasslands (*Pediculari-Seslerietum*) have not lost any species, but have gained 53% of the total number of species occurring during the 32 years of observation; the mesic grasslands (*Luzulo-Festucetum*), on the other hand, have lost 20% of the original species (at 1993) and gained a very high number (81%) of the total number of species occurring during the 25 years of observation. Despite these very relevant changes in species composition, both communities maintain the same total plant coverage values over time (60–70% for *Pediculari-Seslerietum* and 90–95% for *Luzulo-Festucetum).*

The results show different biodiversity features of the two communities (taxonomic and functional) changing over time (Figs 4, 5). The *Pediculari-Seslerietum* community shows an increase in species richness only (even if not significant), while for the *Luzulo-Festucetum* there was an increase in patterns of species richness (significant), evenness and Simpson index (even if not significant), as the result of a clear downward trend in the coverage values of the former dominant species *Festuca violacea* and the invasion or expansion of many opportunistic species, such as *Trifolium pratense.*

As regards morpho-functional features (Figs 6–13), the *Pediculari-Seslerietum* community shows a significant decrease in the leaf width and a significant increase in dense leaf hairs. There are also many significant results associated with the *Luzulo-Festucetum* community: an increase pattern for leaves with sparse hairs and leaf width; a parallel decrease pattern for reclined stems is also discernible. Also traits like graminoid leaves and leaves without hairs show a significant decrease, probably due to the decrease in coverage of *Festuca violacea* (with graminoid leaves) and *Trifolium thalii* (with no hairs on the leaves) and parallel increase of *Trifolium pratense* (with hairs on the leaves).

As far as the analysis of Grime's life strategies (Figs 14–15) is concerned, both the *Pediculari-Seslerietum* and the *Luzulo-Festucetum* communities show an increase in species sharing the stress-tolerant strategy, even if non-significant in the first case.

As regards ecological indicators, generating ecograms of the two plant communities (Suppl. material 1, Figures S5, S6) makes it possible to obtain a graphic image of the ecological niche of each community, narrower in the dry grassland (stress adapted) and larger in the mesic grassland, which however shows a progressive narrowing over time. Indeed, no significant variations over time have been detected for the *Pediculari-Seslerietum* grasslands. On the other hand, the ecological features of the *Luzulo-Festucetum* mesic grasslands show many significant variations over time (Figs 16–17). In detail, our results highlighted a significant increase in the values of the ecological indicators of thermophile behaviour (T), with soil moisture (U) and nitrogen availability (N) decreasing.

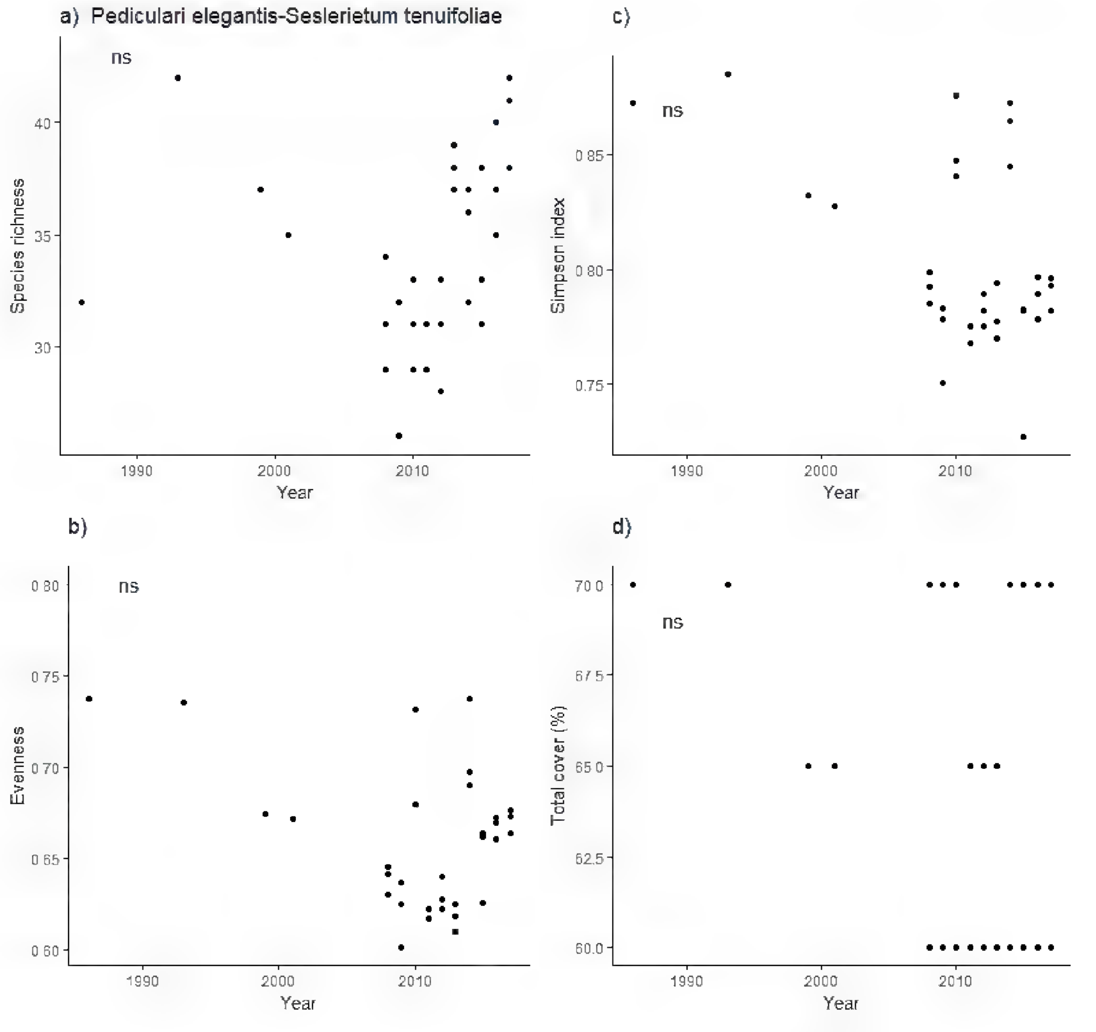

Figure 4. Changes in species diversity traits during the period 1986–2017 (Pediculari-Seslerietum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

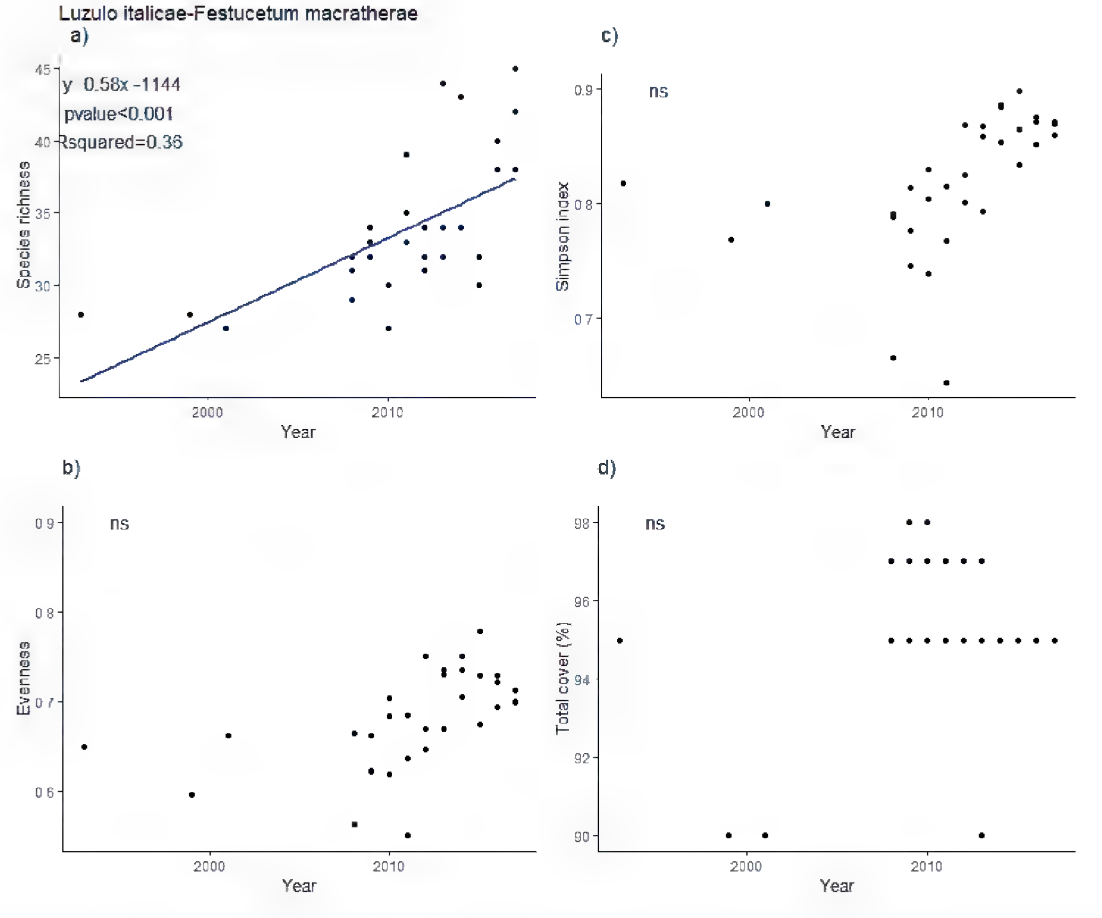

Figure 5. Changes in species diversity traits during the period 1993–2017 (Luzulo-Festucetum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

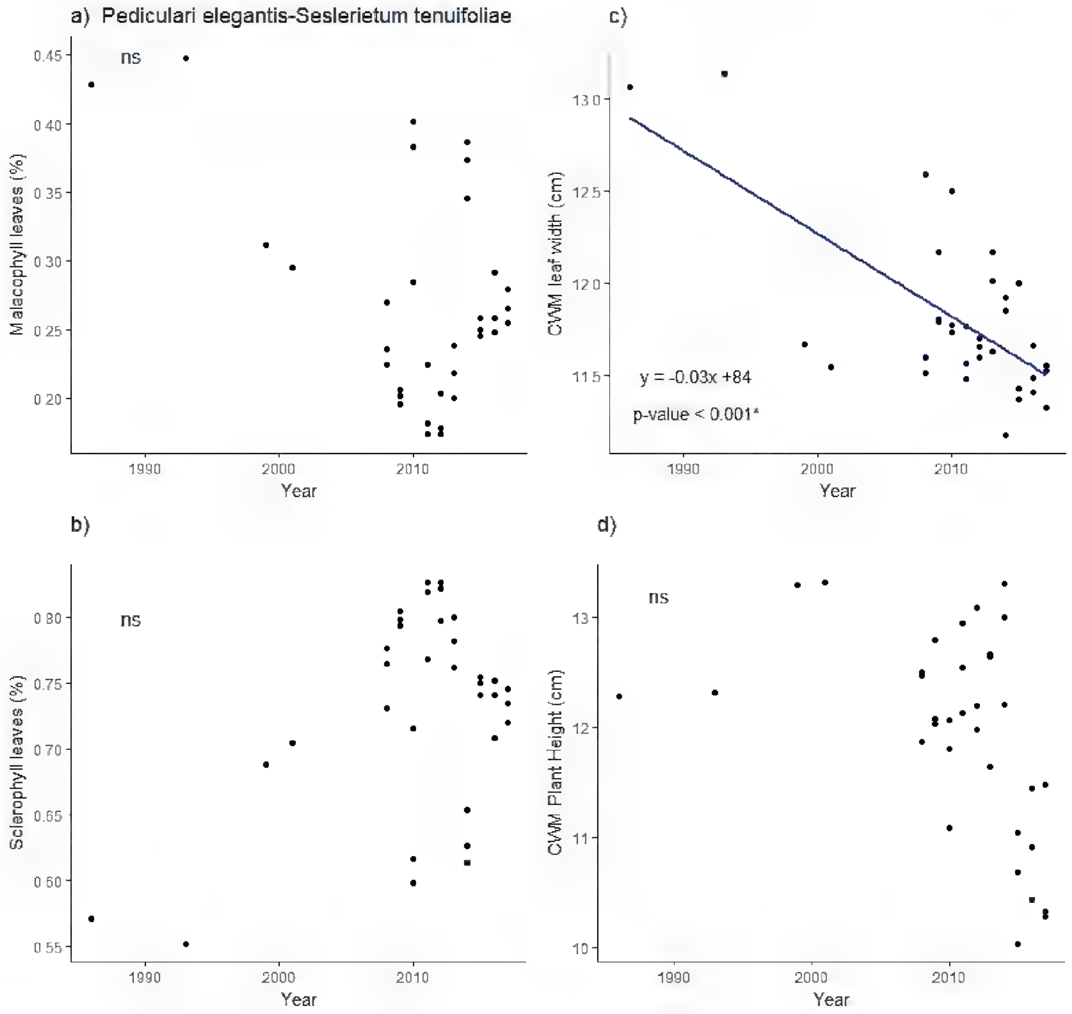

Figure 6. Changes in morpho-functional traits during the period 1986–2017 (Pediculari-Seslerietum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

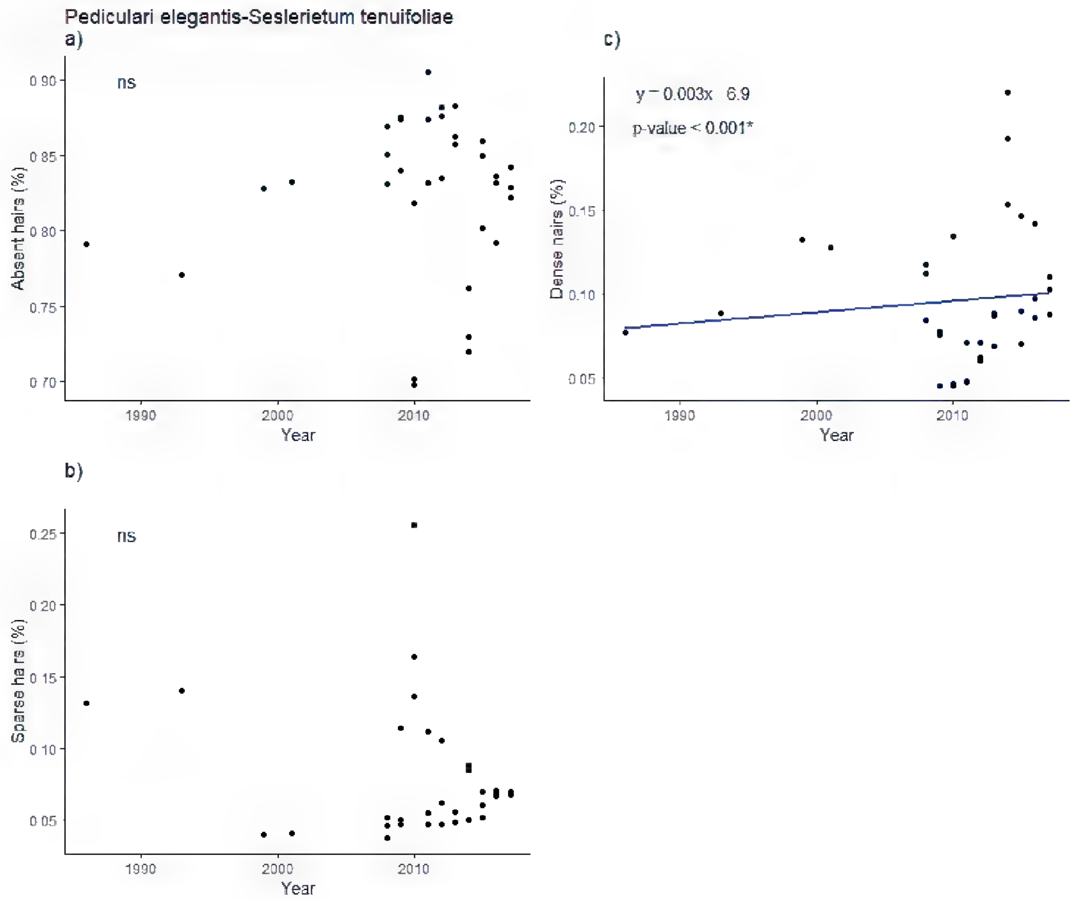

Figure 7. Changes in morpho-functional traits during the period 1986–2017 (Pediculari-Seslerietum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

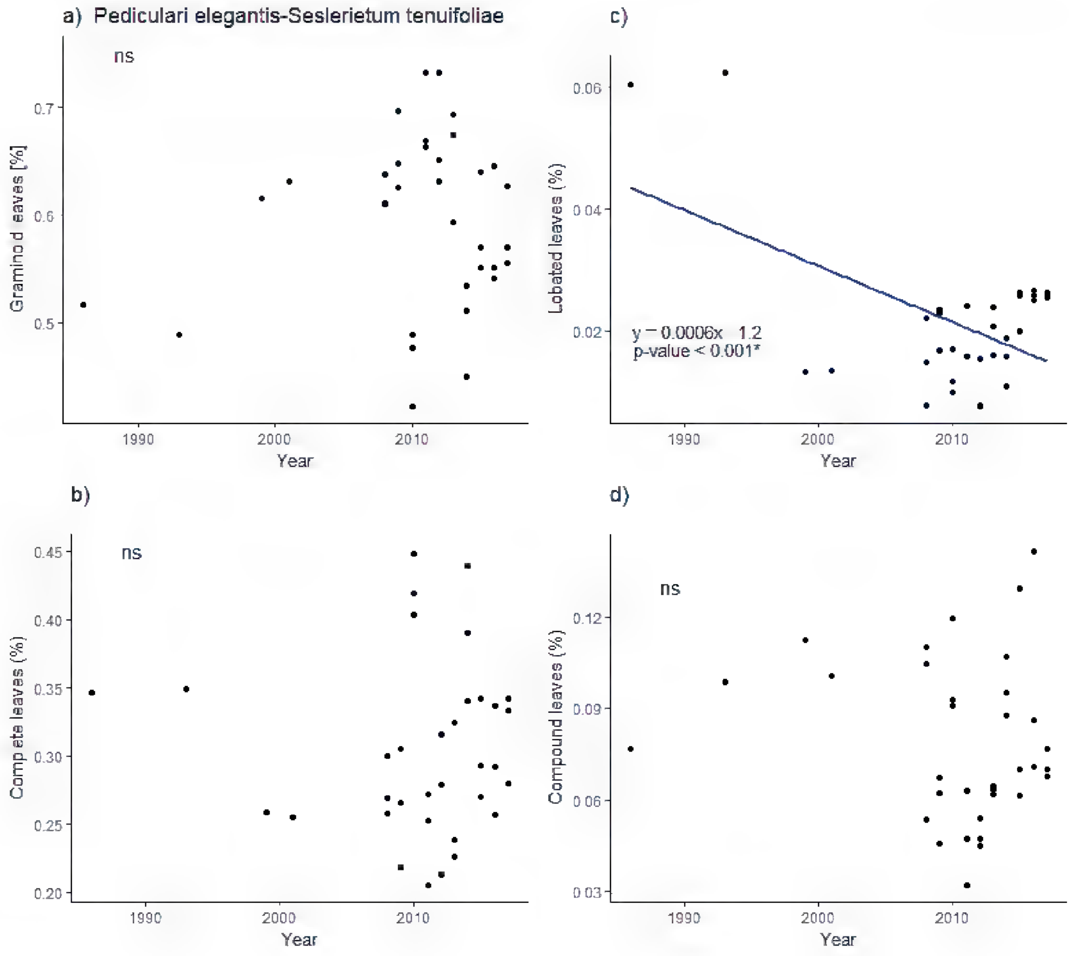

Figure 8. Changes in morpho-functional traits during the period 1986–2017 (Pediculari-Seslerietum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

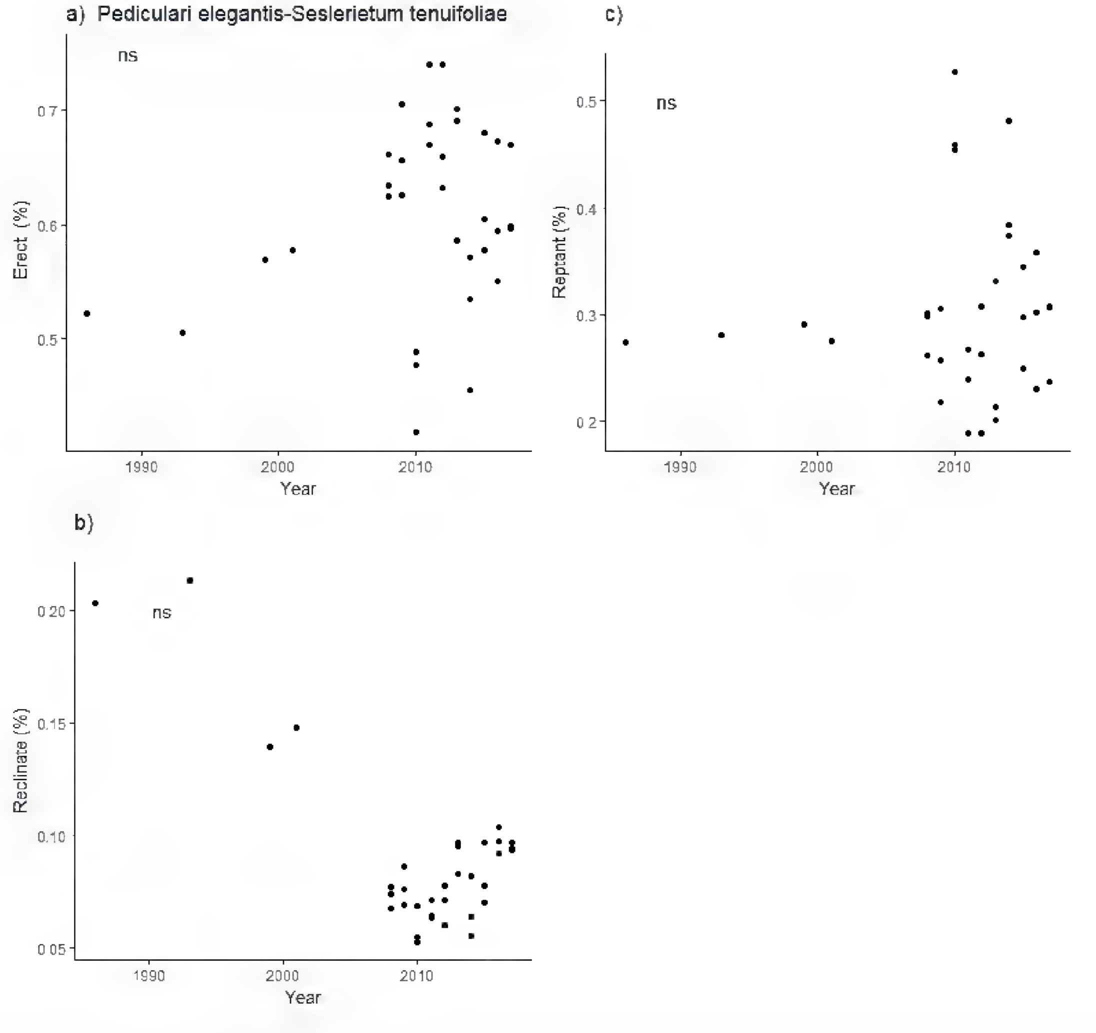

Figure 9. Changes in morpho-functional traits during the period 1986–2017 (Pediculari-Seslerietum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

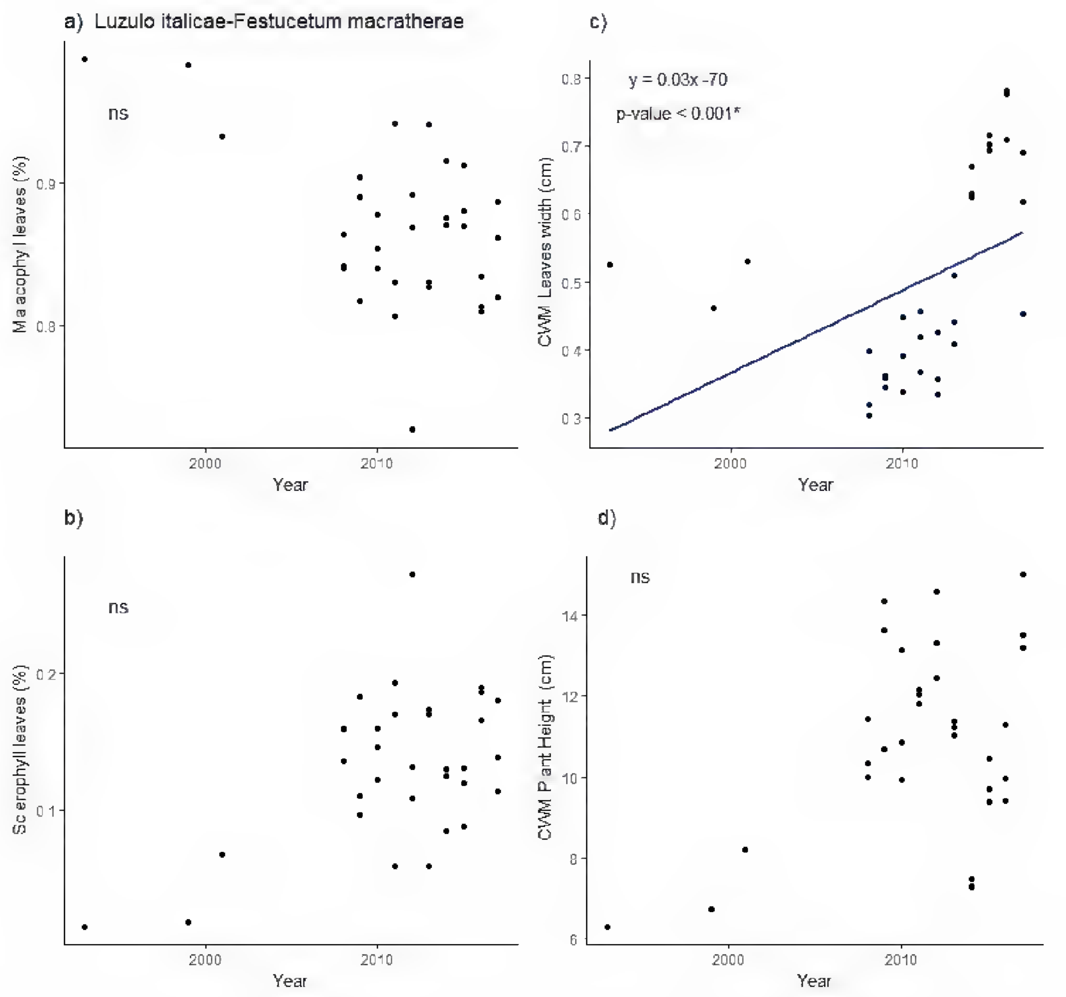

Figure 10. Changes in morpho-functional traits during the period 1993–2017 (Luzulo-Festucetum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

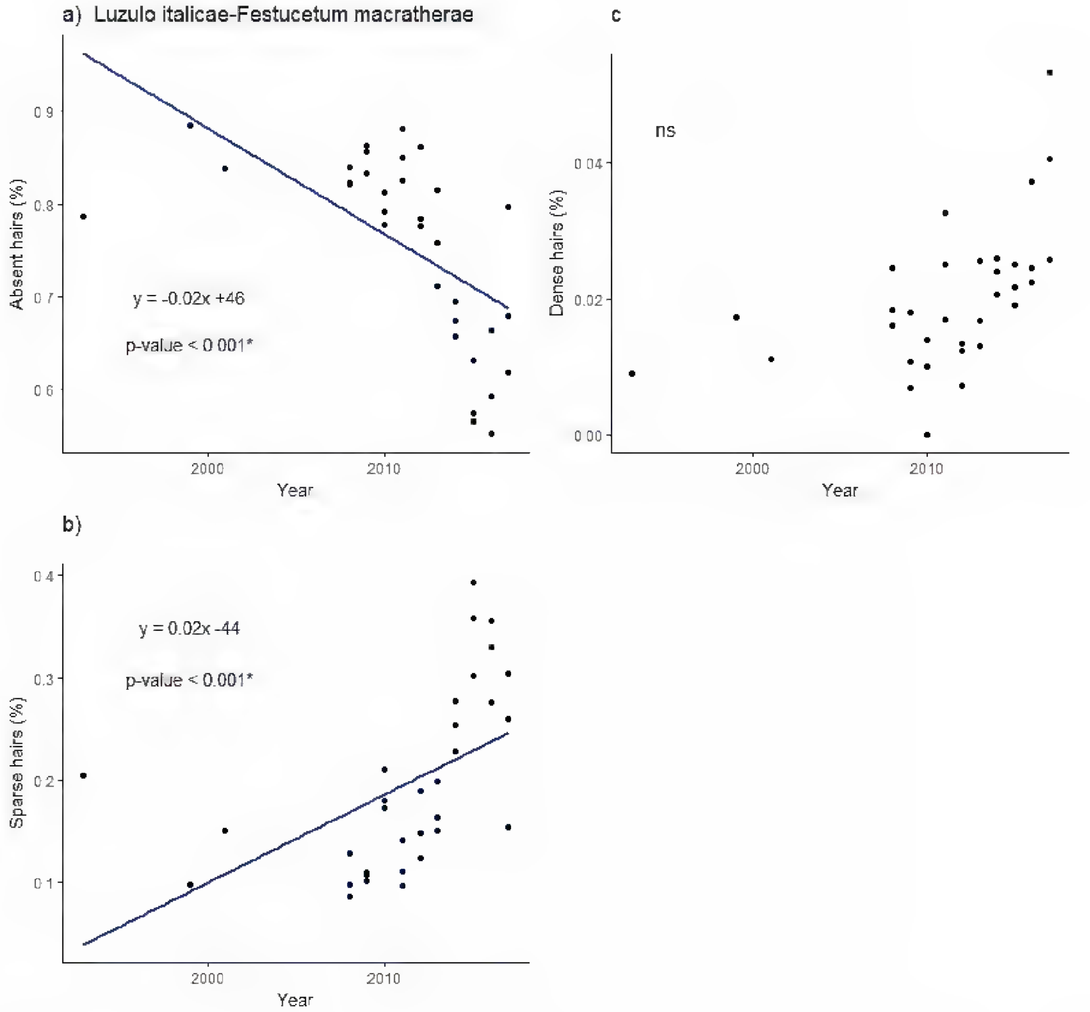

Figure 11. Changes in morpho-functional traits during the period 1993–2017 (Luzulo-Festucetum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

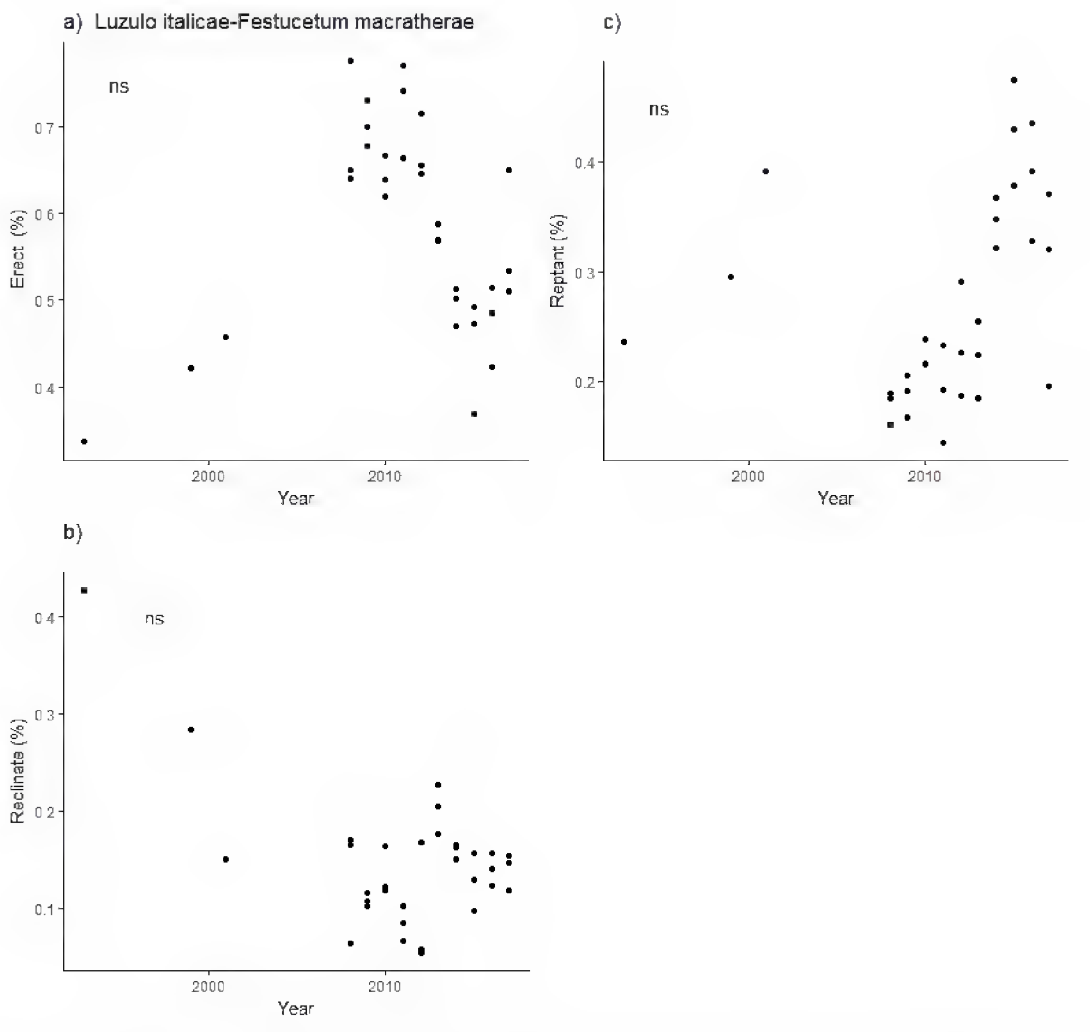

Figure 12. Changes in morpho-functional traits during the period 1993–2017 (Luzulo-Festucetum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

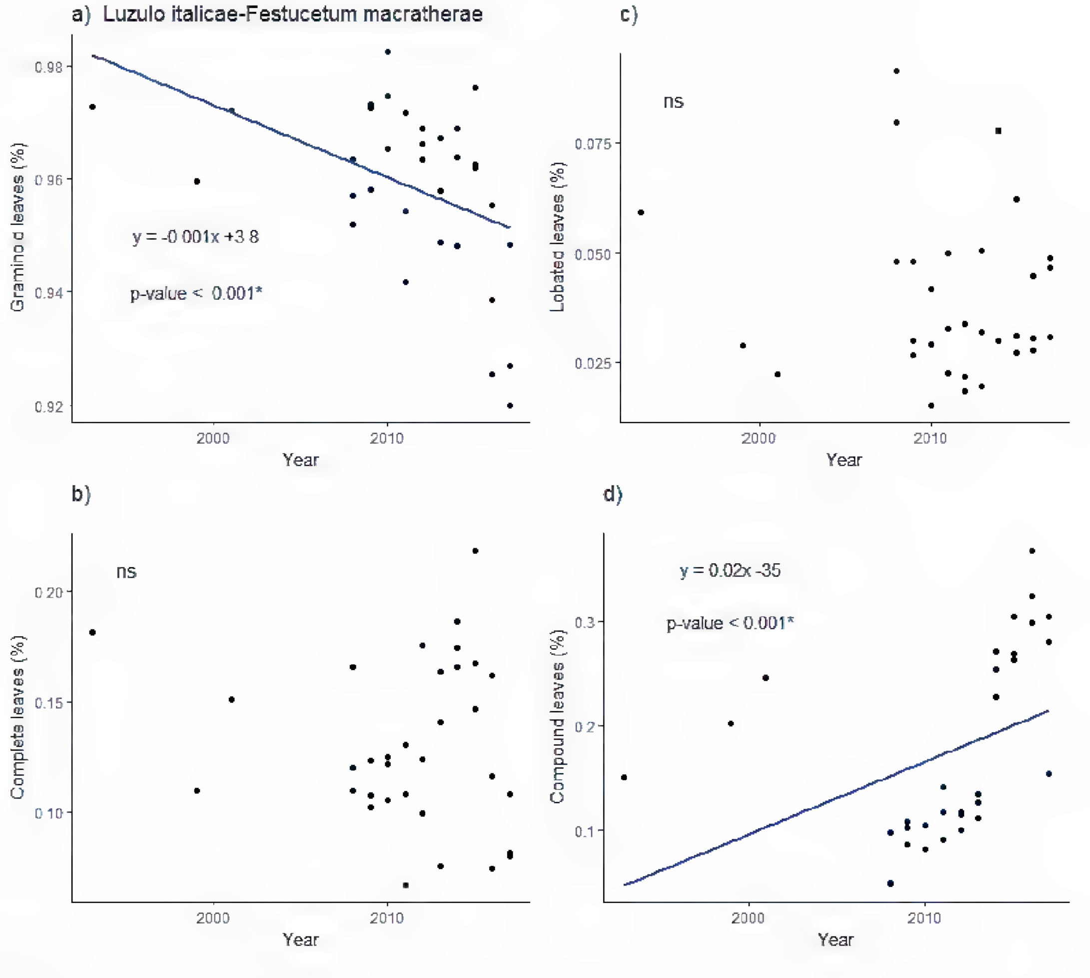

Figure 13. Changes in morpho-functional traits during the period 1993–2017 (Luzulo-Festucetum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

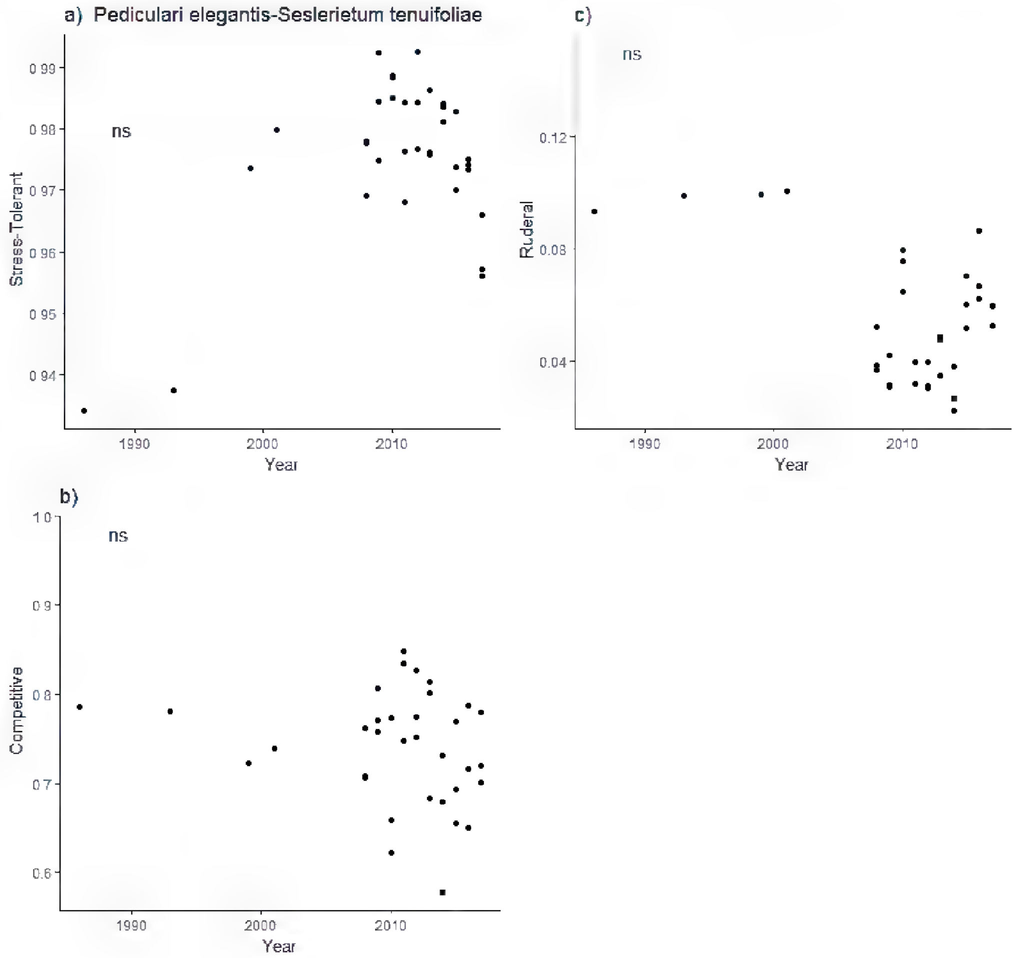

Figure 14. Changes in life strategies during the period 1986–2017 (Pediculari-Seslerietum plots) (S: stress-tolerant; R: ruderal; C: competitive) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

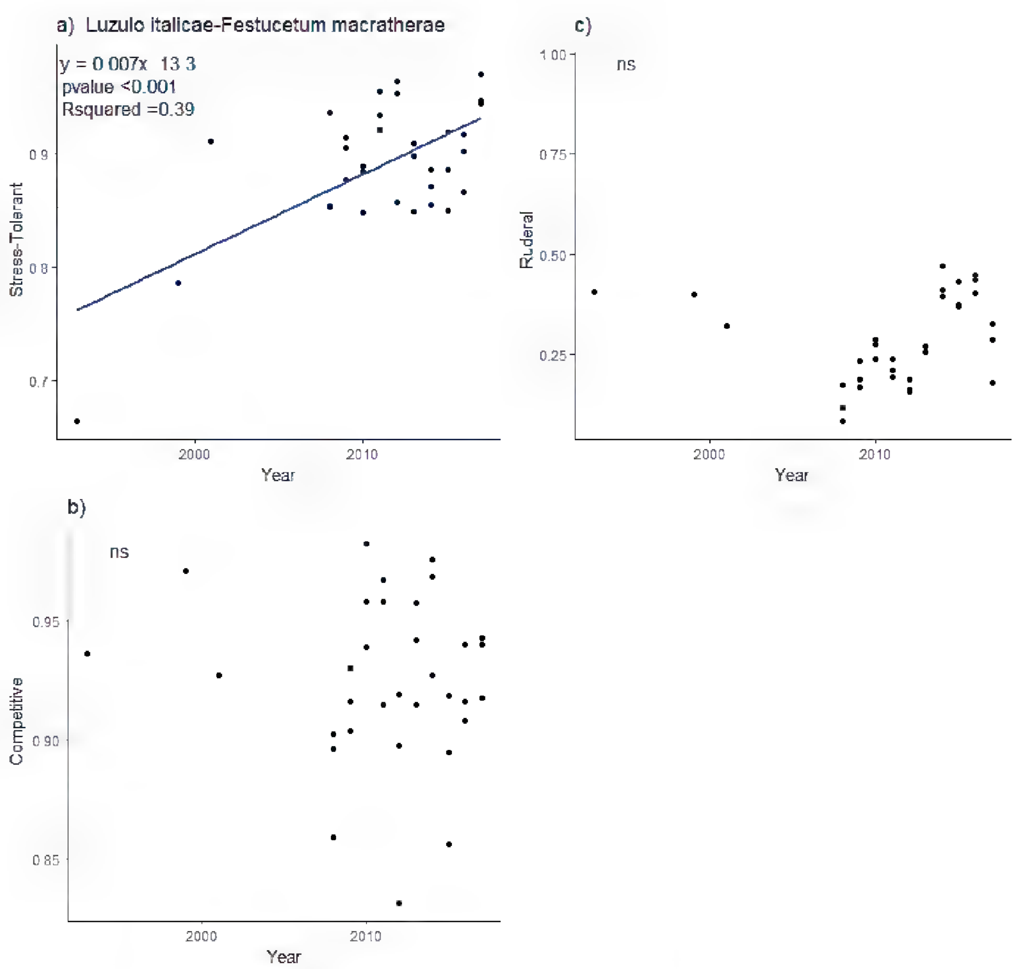

Figure 15. Changes in life strategies during the period 1993)-2017 (Luzulo-Festucetum plots) (S: stress-tolerant; R: ruderal; C: competitive) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

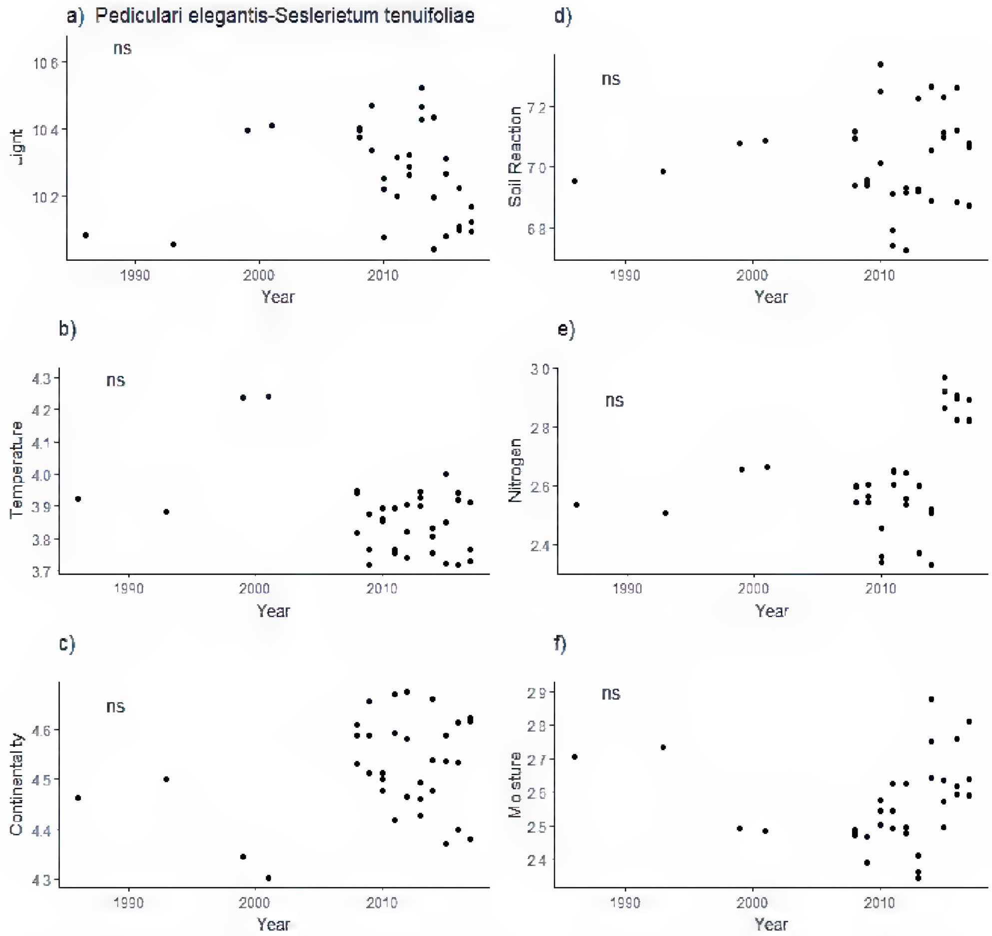

Figure 16. Changes in ecological bioindicator values during the period 1986–2017 (Pediculari-Seslerietum plots) (a): light availability; b): thermophile behaviour; c): continentality gradient; d): pH gradient; e): nitrogen availability; f): soil moisture) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

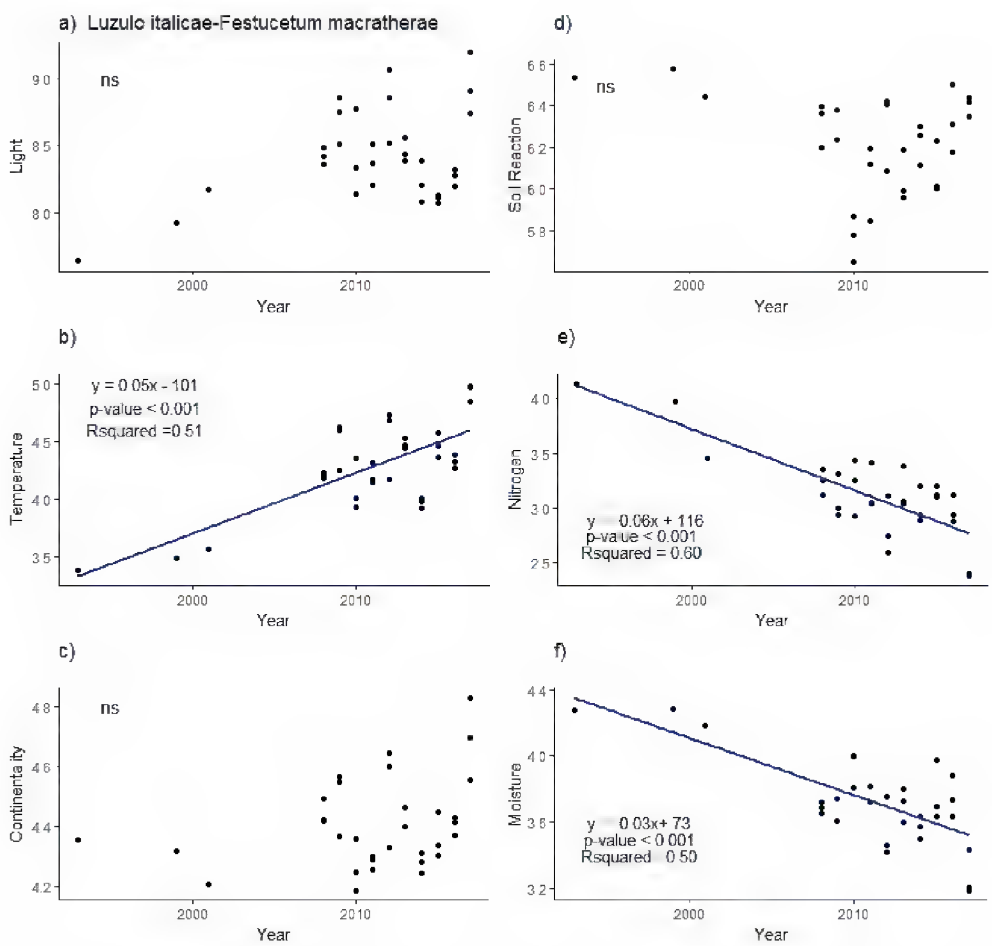

Figure 17. Changes in ecological bioindicator values during the period 1993–2017 at the Gran Sasso d'Italia LTER site (Luzulo-Festucetum plots) (a): light availability; b): thermophile behaviour; c): continentality gradient; d): pH gradient; e): nitrogen availability; f): soil moisture) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

Species level

The results of the analysis at species level highlighted a preferential response for the species belonging to the *Luzulo-Festucetum*, with a lack of response for the selected species of the *Pediculari-Seslerietum*. In detail, a significant decreasing trend has been found for the former dominant species *Festuca violacea* and a significative increasing trend for the new dominant species *Trifolium pratense* and the invaders *Carex caryophyllea* (even if not significant) which have only colonised the community since 2008 (Figs 18–19). On the contrary, *Trifolium thalii* is becoming ever rarer, although no significant trend has been detected.

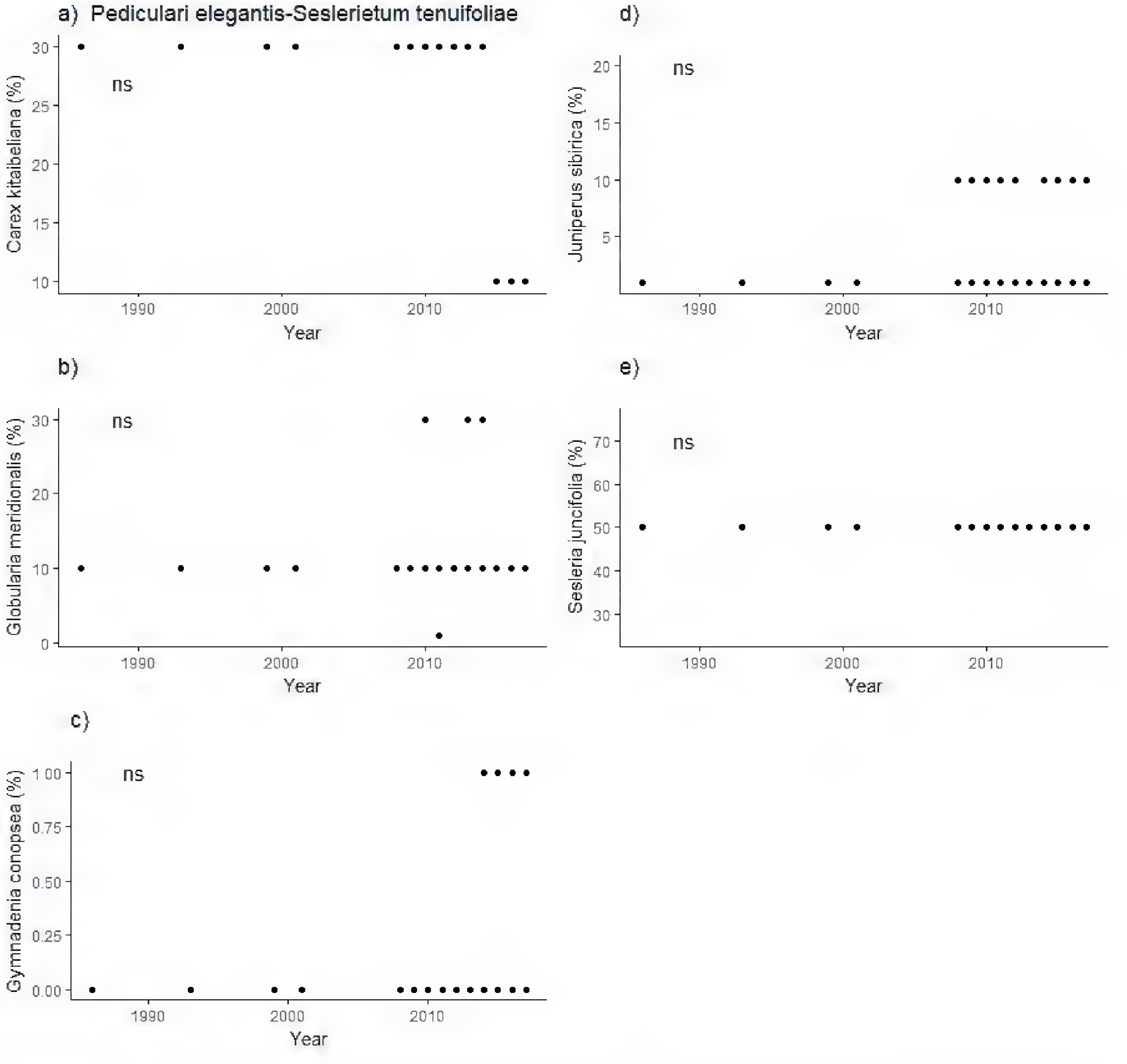

Figure 18. Changes in the coverage values of some selected species (Pediculari-Seslerietum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

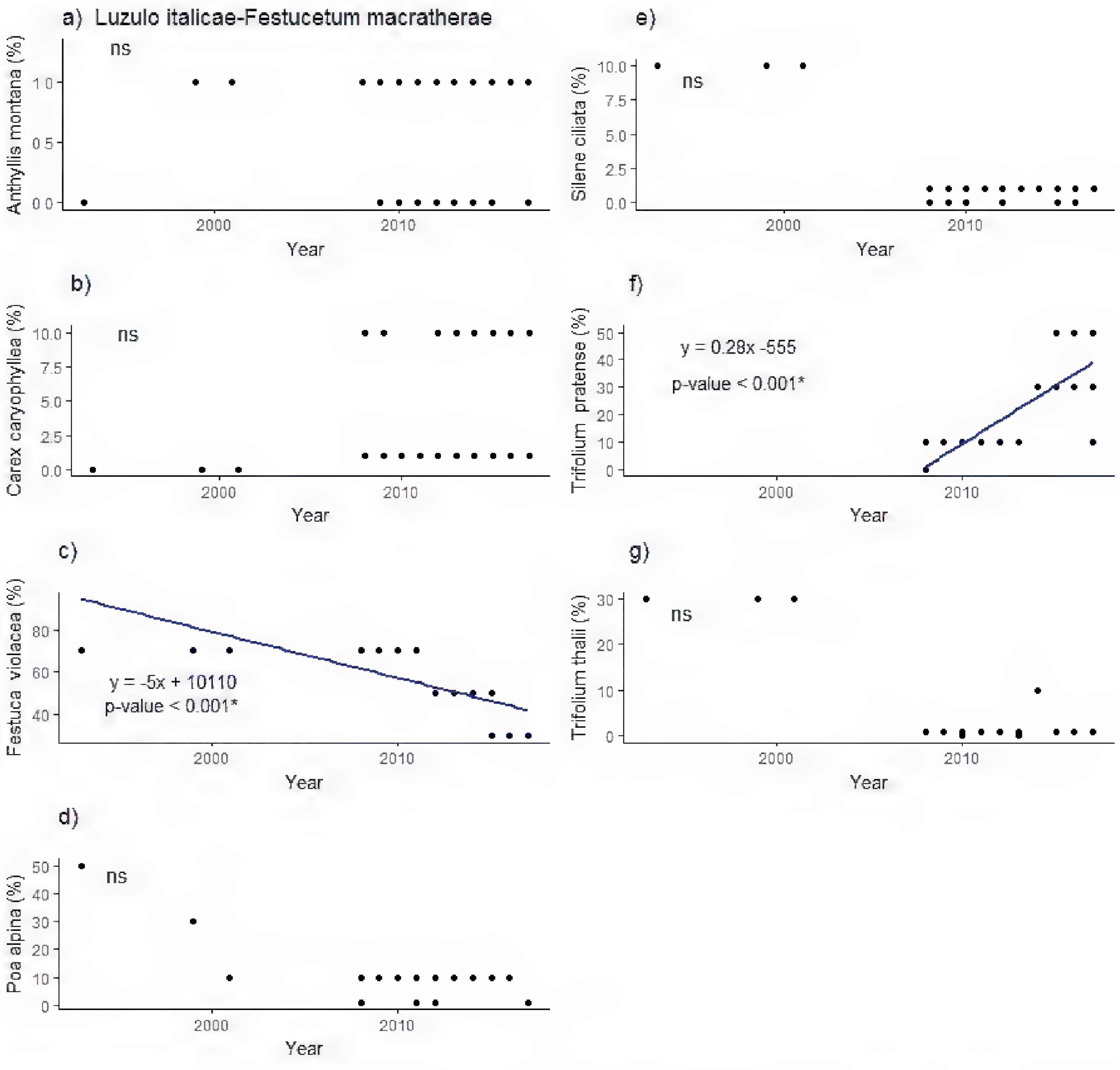

Figure 19. Changes in the coverage values of some selected species (Luzulo-Festucetum plots) (*: regression performed using non-parametric linear regression analysis; ns: non-significant).

Discussion

Climate data are concordant with those presented in Evangelista et al. (2016) for the Central Apennines. The increase in mean annual temperature and very high inter-annual variability in annual precipitation amount are able to produce a strong drought stress in the biocenoses, in particular in very dry years, more and more frequent in the last decades.

Decreased snowfall and snow persistence (and increased variability), together with the variability of total precipitation, increase the ecological stress at the research site, as confirmed by interpretation of the soil microclimate data collected during the last five years: the recorded frequent frost episodes, connected with the absence of protec-

tive snow cover, will expose the biocenoses to very dangerous frost stress. The official meteorological station at the same location (with sensors well above the soil surface) confirms these data, with 167 frost days in winter 2013–2014: only 6 days more than data related to the *Pediculari-Seslerietum* (which therefore remains exposed to frost for a few days only), but 10 days less than data for the *Luzulo-Festucetum* (which conserves the protective snow cover for longer). Decreased snowfall is in agreement with previous observations in the Apennines (Baldoni et al. 1999, Romeo and Scarpelli 2001) and in the Alps (Cannone et al. 2007).

The low yearly rate of species turnover observed at the site (confirming the preliminary results from Petriccione 2005) can be considered physiological in communities in a dynamical stage of fluctuation, such as these, but the long-term analysis shows very significant changes in species composition, with a high increase in the total number of species and a small but relevant lack of sensitive species (in the mesic grassland only). This trend can be seen as an emergent dynamical tendency: early signs of a degeneration process (also highlighted by an increase in invader species) were discernible after just seven observation years and were confirmed in subsequent years. Signs like these are more evident in snow-dependent communities *(Luzulo-Festucetum)*, more sensitive to drought increase and snow cover shortage.

Although both communities preserve the same values of total plant coverage over time, in the case of the *Luzulo-Festucetum* the former dominant species (*Festuca violacea*) lost its past role, due to the invasion and expansion of an opportunistic species (*Trifolium pratense*). These results are in good agreement with those found in the Central Italian Alps in the subalpine, alpine and nival belts over the last 50 years (Cannone and Pignatti 2014), but they contrast with the vegetation coverage increase noted for many species in other Alpine ranges and for other LTER sites in the Central Apennines during the last 20 years (Rogora et al. 2018).

The significant changes of morpho-functional traits, noted in both communities, are interpretable as the effects of a decrease of snow cover and an increase in temperature and drought stress (Körner 1994) Small leaves (decrease in leaf width was found in the *Pediculari-Seslerietum* dry grassland) in fact reduce boundary layer resistance and help maintain favourable leaf temperatures and higher photosynthetic water-use efficiency-with high solar radiation and low water availability (Givnish 1987; Knight and Ackerly 2003). An increase in species with dense hairs could also be the result of drought stress adaptation over time. Hairs, in fact, protect plant species from solar intensity, but also retain air moisture and avoid water loss from the plant (Wagner et al. 2004).

Regarding the *Luzulo-Festucetum* mesic grassland, on the other hand, we found a more complex response to the variation over time. In line with the trend of increasing drought, we noted a significant decrease in species without hairs and a significant increase in species with sparse hairs. The observed increase of leaf width is apparently in contrast with increasing drought stress. However, this pattern may be the result of an increase in compound leaves, given that for these species the leaf, and not the leaflet, was measured. An increase in compound leaves along the aridity gradient has been noted (Givnish 1978) and leaves along a deciduous rachis are probably advantageous in dry environments.

The significant changes in life strategies, with an increase in species with a stress-tolerant strategy for the mesic community, are characteristic of biocenoses with increased ecological stress, undergoing changes towards adaptation to an increased drought. These results are in agreement with observations made in the Alps (Chapin et al. 1996, Theurillat and Guisan 2001, Welker et al. 2001, Cannone et al. 2007).

The progressive narrowing of the *Luzulo-Festucetum* ecogram over time confirms the correlation between the observed warmth and drought trends and the related changes in the sensitive mesic plant community. Our results exclude a possible effect on changes in vegetation caused by modified land use or nitrogen accumulation in the soil (as shown by the related ecogram, with a clear decrease in nitrogen availability indicators over time), unlike the assumptions of Evangelista et al. (2016).

Dry grassland shows higher resistance to an increased drought than mesic grassland. To improve the reliability of the findings, a regression model (non-parametric where assumptions were not met) removing data collected before 2008 (with no replicates) was also performed (Suppl. material 1, Table S3). The ecological meaning of the results is very similar, showing the preferential response of mesic grassland towards drought adaptation and the lower variation of dry grassland, again towards aridity.

Conclusions

The warming trend at global level is confirmed and reinforced by data related to the LTER site "Gran Sasso d'Italia": the mean annual temperature has increased by 1.7 °C over the last 65 years, corresponding to an average increase per decade of +0.26 °C. This is more than double the same values at global level (+0.7 °C in the last 60 years and +0.1 °C per decade, IPCC 2014), and very near the forecasted increase of +2.0° C by the year 2100 (IPCC 2014).

This exceptional warming in alpine areas, together with a decrease in total precipitation (as recognized for the Central Apennines as a whole, even if not significant at the site) and snowfall (significant at the site), an increase in climate inter-annual variability and extreme events, and a frequent lack of snow cover, are the combined drivers of the intense species turnover observed, occurring over the last 30 years in all the biocenoses studied, although more marked in snow-dependent communities. A quantitative increase in more thermophilic and stress- and drought-tolerant species and a parallel decrease in more mesic, cold adapted and competitive species have been clearly detected. These results confirm the preliminary assumptions provided in Petriccione (2012) for the first 18–25 years of observation at the same LTER site.

Ecological indicators demonstrate that the key factor in the ecological changes of the alpine biocenoses studied is drought, associated with the combined action of temperature increase, precipitation decrease and lack of snow cover and precipitation.

The two communities studied react in different ways to these abiotic drivers: (1) the *Pediculari-Seslerietum* dry grassland, highly resistant and well adapted to drought, frost and drastic temperature ranges, shows very slow or no changes over time (in accordance with the results of Frate et al. 2018); (2) the *Luzulo-Festucetum* mesic grass-

land, with low resistance (increase in species richness and invaders) and not adapted to drought and soil frost, shows important and rapid changes, increasing cover values for species with ruderal and stress-tolerant strategies, and a parallel decline in the former dominant species, towards first signs of drought stress.

The fluctuation stage typical of these primary alpine plant communities seems to be changing toward a dynamical tendency of degeneration, with an important disgregation of the community due to deterioration of the ecological connections: as in the Central Alps, this process can lead to an ecological vacuum or a disequilibrium state in the biocenoses (Cannone and Pignatti 2014).

In conclusion, our results enable us to answer the four questions listed in the introduction: a) plant communities are significantly changing over time, more for mesic grassland and less for dry grassland; b) toward a disequilibrium state; c) species are responding in different ways, altering the intra-community ecological connections; d) there is a relationship between the changes in the features of the communities and the predicted and the observed changes in the temperature and precipitation regimes.

Additional long-term observations over the next decades are, in any case, required to confirm the hypothesis of a cause-effect relationship between climate change and changes in plant communities and to exclude natural and unknown fluctuations.

The combined monitoring of vegetation (composition and structure) and temperature at high elevation will provide updated data on the processes currently underway on the high summits of the Apennines and will guide the local in-situ policies to conserve the associated plant communities and threatened species.

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Supplementary material 1

Supplementary tables and figures

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Data type: measurements

Explanation note: **Table S1.** Pediculari-Seslerietum 1986–2017 (phytosociological releves). **Table S2.** Luzulo-Festucetum 1993–2017 (phytosociological releves). **Figure S1.** Geographical location of the LTER site "Gran Sasso d'Italia" (site area in pink; permanent plots indicated by red squares). **Figure S2.** Pedological profile of the Gran Sasso d'Italia Pediculari-Seslerietum community (soil depth in cm; from Furrer and Furnari 1960). **Figure S3.** Pedological profile of the Gran Sasso d'Italia Luzulo-Festucetum community (soil depth in cm; from Furrer and Furnari 1960). **Figure S4.** Changes in snow abundance during the period 1988-2016 (mean winter snow depth, in cm; total winter snow precipitation, SWE in mm*. 1cm of snowfall was assumed equal to 1mm snow water equivalent). **Figure S5.** Changes in the ecogram during the period 1986-2017 for the Pediculari-Seslerietum dry grassland plots (L: light availability, T: thermophile behaviour, C: continental gradient, U: soil moisture, R: pH gradient, N: nitrogen availability). **Figure S6.** Changes in the ecogram during the period 1993-2017 for the Luzulo-Festucetum mesic grassland plots (L: light availability, T: thermophile behaviour, C: continental gradient, U: soil moisture, R: pH gradient, N: nitrogen availability). **Table S3.** Results of statistical analysis based on data only from 2008 with replicates. Positive or negative slope coefficient refers to increase or decrease of given traits or indices. Parametric model refers to linear model (lm function in package stats), while non-parametric model refers to median based linear model (mblm function in package mblm). Only parametric model gives R2.

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